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Differential oviposition and offspring success of gray treefrogs in the presence of an invasive fish

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Abstract. Females often decide where to place their eggs or offspring based on the relative risks and benefits of a location. One trade-off may be between ovipositing with predators and ovipositing with competitors. Many amphibians show risk-sensitive oviposition and select oviposition sites based on offspring performance. We examined differential oviposition and offspring success by gray treefrogs (*Hyla versicolor*) in response to the presence of caged or free-ranging invasive western mosquitofish (*Gambusia affinis*) using cattletank mesocosms as experimental ponds. Our experiment sought to answer these questions by comparing the number of eggs laid and tadpoles produced among the experimental treatments: (1) Do gray treefrogs exhibit risk-sensitive oviposition? and (2) What is the relative importance of pre-colonization and post-colonization consumptive and trait-mediated effects of western mosquitofish? Gray treefrogs laid more eggs in control and caged predator mesocosms than in free-ranging predator mesocosms. At the end of the experiment, there were more tadpoles in control and caged predator mesocosms than in free-ranging predator mesocosms. Proportional yield was lower in free-ranging predator mesocosms than control and caged predator mesocosms. Eggs were laid 7–8 d earlier in control mesocosms than caged and free-ranging predator mesocosms. Western mosquitofish therefore had a negative effect on the successful colonization of experimental ponds by gray treefrogs, most likely through direct physical interactions. Our results also suggest gray treefrogs shift oviposition preferences as the number of conspecifics reaches a threshold where competition risk outweighs predation risk. Western mosquitofish therefore have great potential to affect the distribution of gray treefrogs through pre- and post-colonization effects.

Key words: competitor; *Gambusia affinis*; *Hyla versicolor*; post-colonization effects; pre-colonization effects; predator; risk sensitive; threat sensitive.

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INTRODUCTION

Ovipositing females in heterogeneous habitats must make decisions about where to place their eggs or offspring based on the relative risks and benefits found in each habitat type. One trade-off may be between avoiding ovipositing in the presence of predators and avoiding ovipositing in the presence of competitors. For example, Kershenbaum et al. (2012) found that below a certain larval density, adult mosquitoes avoid sites with predators, but above that threshold, they use

both predator and predator-free sites; thus, mosquitoes may be evaluating competition risk vs. predation risk, and ultimately may choose predator sites over high competition sites (Silberbush et al. 2014). In other words, the ovipositing females are choosing their oviposition sites to maximize fitness as expected from the ideal free distribution (Fretwell and Lucas 1970). Indeed, Blaustein (1999) posited, based on a review of the literature on mosquito oviposition choice, that the relative risk of predator-free habitats compared to habitats with predators changes with conspecific

density such that at some threshold conspecific density, habitats with predators are more attractive than predator-free habitats with high conspecific densities.

Amphibians have been shown to exhibit risk-sensitive oviposition (reviewed in Buxton and Sperry 2017) and to select oviposition sites on the basis of offspring or larval performance (Freidenburg 2017, Pintar and Resetarits 2017). Previous studies on oviposition site choice in anurans have shown that both fish predators and the presence of conspecific eggs or tadpoles can independently affect oviposition site choice, especially species in the family Hylidae (reviewed in Buxton and Sperry 2017). For example, several studies found that *Hyla* spp. tend to avoid ovipositing in experimental ponds with caged or non-lethal fish predators (Binckley and Resetarits 2008, Vonesh et al. 2009, Kraus and Vonesh 2010, Kraus et al. 2011). In addition, post-colonization effects in ponds with lethal fish predators frequently greatly reduce or eliminate any eggs or tadpoles that were oviposited in the ponds (Rieger et al. 2004, Vonesh et al. 2009). Thus, fish predators can reduce initial colonization but also exert strong post-colonization effects on anurans. Several studies also show that females prefer to lay their eggs in aquatic habitats with no or few conspecific eggs or tadpoles, most likely as a way to avoid competition or cannibalism (Resetarits and Wilbur 1989, Rieger et al. 2004, Schulte et al. 2011, Stein and Blaustein 2015, Cayuela et al. 2016). However, some species select oviposition sites with other conspecific eggs or tadpoles, perhaps because they may be a cue to lower or reduced predation risk compared to other habitats with no conspecifics (Murphy 2003, Rudolf and Rödel 2005).

It might therefore be predicted that oviposition site selection by amphibians should show a similar change to that described by Blaustein (1999) for mosquitoes. For example, as the number of conspecifics, either eggs or tadpoles, increases in predator-free ponds, the risk of competition increases. At some point, this risk of competition likely outweighs the risk of predation. Therefore, adults may choose to oviposit in predator habitats. Evidence for such shifts exists in anurans. When eggs were removed daily, *Hyla chrysoscelis* and *Hyla squirella* only oviposited in the presence of a fish predator on nights with the highest

breeding activity (Binckley and Resetarits 2003, 2008). In contrast, Resetarits et al. (2018) found no evidence of conspecific density affecting the avoidance of ponds with fish in *H. chrysoscelis*, but eggs were removed daily for the first 31 d of the 71-d experiment (44% of the experiment). However, the prediction of a shift in oviposition site selection has not been directly tested since in these previous studies, eggs have been removed in the experimental habitats soon after they were deposited for much or all of the duration of the experiment.

One particular fish predator, the invasive western mosquitofish (*Gambusia affinis*), has significant impacts on aquatic communities despite its relatively small size (adults <60 mm total length; reviewed in Pyke 2008). Mosquitofish (*G. affinis* and *G. holbrooki*) consume a variety of native tadpoles where they have been introduced (Pyke 2008, Remon et al. 2016, Vannini et al. 2018). Many hylid species avoid or reduce oviposition in bodies of water with *G. affinis* (e.g., *Litoria aurea*, Pollard et al. 2017; *Pseudacris triseriata*, Buxton et al. 2017; *H. chrysoscelis*, Binckley and Resetarits 2003). In addition, the abundances of hylid tadpoles are frequently lower in the presence of *G. affinis*, either in mesocosms or in constructed wetlands (Preston et al. 2012, 2017, Shulse et al. 2013, Fryxell et al. 2015), although this is not always the case in natural wetlands (Preston et al. 2017).

We examined the potential for differential oviposition and offspring success by gray treefrogs (*Hyla versicolor*) in response to caged and free-ranging invasive western mosquitofish (*G. affinis*). In addition, we examined whether the response to the presence of the western mosquitofish changed over time as conspecific eggs and tadpoles occurred in the experimental ponds. Our experimental design also allowed us to look at how the caged and free-ranging presence of western mosquitofish affects the production of gray treefrog tadpoles through post-colonization effects. We hypothesized that if gray treefrogs were exhibiting risk-sensitive oviposition, they would lay more eggs in the control mesocosms without fish followed by the caged predator mesocosms and then the free-ranging predator mesocosms. We also hypothesized that if post-colonization consumptive effects of fish were important, then the proportion of eggs laid in a

mesocosm that produced living tadpoles at the end of the experiment (proportional yield) would be lowest in the free-ranging predator treatments and there would be higher and similar yields in the control and caged predator treatments. Alternatively, if post-colonization consumptive and trait-mediated effects of fish were important we hypothesized that proportional yield would be lowest in the free-ranging predator mesocosms, intermediate in the caged predator mesocosms, and highest in the control mesocosms.

MATERIALS AND METHODS

We established an array of 18 experimental ponds using Rubbermaid stock tanks, filled with 800 L of well water on 9 May 2011. The 18 tanks were placed into six blocks with one replicate of each treatment per block. Upon filling, we added 8 L (≈ 500 g) of mixed deciduous leaf litter to each mesocosm. On 10 May 2011, we inoculated each mesocosm with water from local ponds that was filtered through 1-mm mesh screening to eliminate any macroinvertebrates, and added 25 g of rabbit chow (Purina, St. Louis, Missouri, USA) to provide initial nutrients. Mesocosms were covered with fiberglass screening prior to the start of the experiment to allow for development of algae and zooplankton while preventing colonization.

In each mesocosm, we placed a 32-gallon (121-L) plastic garbage can with four windows (each 9×12 cm) cut into its sides below the water line. We created three predator treatments (each replicated 6 times). (1) Control: windows left open with fiberglass window screening (1-mm mesh) siliconed to the inner wall of the garbage can, but not covering the openings. (2) Caged predator: windows covered with fiberglass window screening (1-mm mesh) and 5 mosquitofish (two males and three females) placed in the garbage can, allowing chemical cues from the fish to circulate throughout the mesocosm but preventing the fish from physically accessing the majority of the mesocosm. (3) Free-ranging predator: windows open as in the Control treatment, with 5 mosquitofish (two males and three females) placed in the garbage can, allowing the fish to use the entire mesocosm, providing chemical cues, and potentially consuming colonizing organisms. Male mosquitofish were 20–30 mm TL, and female mosquitofish were 45–55 mm TL.

The experiment began on 1 June 2011 with the removal of the fiberglass screening covering the mesocosms and the addition of mosquitofish. We monitored mesocosms daily for 6 weeks (2 June–14 July), counting the number of gray treefrog eggs oviposited in each mesocosm every morning. To minimize disturbance of egg masses and mesocosms, egg counts were done by eye using a handheld counter to aid making counts. We carefully searched each mesocosm for egg masses. Gray Treefrog females lay eggs in multiple small clusters of eggs ranging in size from 30 to 40 (Cline 2005). The small sizes of each cluster made counting by eye easier than for other types of egg masses. We did not remove eggs from the mesocosms, allowing the eggs to potentially produce tadpoles. We were able to differentiate eggs laid on each day by changes in the appearance of eggs and their jelly coating. We are also confident that our egg counts in the free-ranging predator treatments were not affected by consumption by the mosquitofish because (1) the time between oviposition and counting was <10 h, most of which was at night. Mosquitofish use visual cues in foraging (Russo et al. 2008 and references therein), and show a morning peak in foraging (Pyke 2005); thus, the opportunity for consumption is likely limited given the timing of our daily surveys, and (2) *G. affinis* do not appear to consume gray treefrog eggs, at least in our study population (Smith and Smith 2015). On 14 July, we removed and counted all surviving tadpoles and fish (both adults and offspring) from each mesocosm by dipnetting and draining each mesocosm. In our daily checks of the mesocosms, we observed no metamorphs, nor did we observe any tadpoles at the end of the experiment that were close to metamorphosis; thus, we are confident that our final counts of tadpoles were not affected by escaped metamorphs. We excluded three mesocosms from our analyses that experienced red algae blooms (one control and two free-ranging predator).

We analyzed the effects of the predator treatments on the total number of eggs laid in a mesocosm and total number of tadpoles surviving in each mesocosm. In addition, we calculated the mean day of the experiment on which eggs were laid and the proportion of eggs that produced surviving tadpoles at the end of the experiment (proportional yield: tadpoles counted in a

mesocosm at end of experiment/total number of eggs laid in the mesocosm). We log-transformed the total number of eggs and tadpoles to meet the assumptions of ANOVA prior to analyses. We transformed proportion data (i.e., proportional yield) using an arcsine square root transformation. For clarity, we report untransformed means. Assumptions for parametric tests were confirmed with the Shapiro-Wilk W-tests (normality) and Levene's tests (equal variances). We used one-way ANOVAs to analyze the dependent variables and used Tukey's HSD post hoc tests to compare treatment means for significant ANOVAs. We initially included a block factor in all analyses, but removed it from the final model if it was not significant (if no block effect is reported, it was not significant). We used an α -value of 0.05 for significance. We used JMP Pro 13 for the analyses (SAS Institute, Cary, North Carolina, USA).

RESULTS

Over the course of the experiment, we counted a total of 18,115 eggs across all mesocosms (7799 in control, 8466 in caged predators, and 1850 in free-ranging predator). At the end of the experiment, we removed a total of 5257 tadpoles across all mesocosms (3291 in control, 1907 in caged predator, and 59 in free-ranging predator).

More eggs (log-transformed) were laid over the course of the experiment in control and caged predator mesocosms than in the free-ranging predator mesocosms (Fig. 1A; $F_{2,12} = 5.07$, $P = 0.025$). There were also more tadpoles at the end of the experiment (log-transformed) in the control and caged predator mesocosms than there were in the free-ranging predator mesocosms (Fig. 1B; $F_{2,12} = 23.17$, $P < 0.0001$).

The proportional yield was greater in control and caged predator mesocosms than in the free-ranging predator mesocosms (Fig. 1C; $F_{2,5} = 13.74$, $P = 0.0093$). Block had a significant effect on proportional yield ($F_{5,5} = 8.95$, $P = 0.016$). The mean day eggs were laid was earlier in the control mesocosms than in the caged and free-ranging predator mesocosms (Fig. 1D; $F_{2,5} = 22.18$, $P = 0.0033$). Block had a significant effect on the mean day egg masses were deposited ($F_{5,5} = 16.65$, $P = 0.004$).

When considering only the two treatments with western mosquitofish, we recovered

significantly more fish from the free-ranging predator treatment (64.5 ± 22.9 fish, $N = 4$; range = 37–133 fish) than from the caged predator treatment (7.83 ± 0.75 fish, $N = 6$; range = 6–11), with evidence of reproduction in both treatments (i.e., more fish than stocked; $F_{1,8} = 9.77$, $P = 0.014$). The excess fish were all very small juveniles (≤ 10 mm total length), and in the caged treatments, none were observed outside the caged areas. Higher rates of cannibalism of the caged mosquitofish are likely the explanation for the observed differences in apparent reproduction (see Rettig et al. 2018 for evidence of cannibalism in this population of western mosquitofish).

DISCUSSION

Our results, in general, support the hypotheses that the gray treefrogs exhibited risk-sensitive oviposition and that post-colonization consumptive effects resulted in reduced tadpole success. Our experiment clearly demonstrates that the presence of western mosquitofish had a negative effect on the ability of gray treefrogs to successfully colonize experimental ponds and produce tadpoles. In particular, the numbers of eggs oviposited and tadpoles produced were reduced in the free-ranging predator treatments compared to the caged predator and control treatments. These results strongly suggest that the impact of western mosquitofish was due to direct interactions between the fish predator and the gray treefrogs since the effect was only seen in the free-ranging predator treatments. However, our results also suggest that colonization was deterred in the caged predator treatments relative to the control treatments, as suggested by the difference in the mean day of oviposition of gray treefrogs in the different predator treatments. Finally, our results indicated that both pre- and post-colonization effects were responsible for the effects of western mosquitofish on the successful production of tadpoles in the experimental ponds by the gray treefrogs. Below we will address each of these results in turn.

Western mosquitofish effects on oviposition by gray treefrogs

Gray treefrogs laid significantly fewer eggs over the course of the experiment (roughly one-third

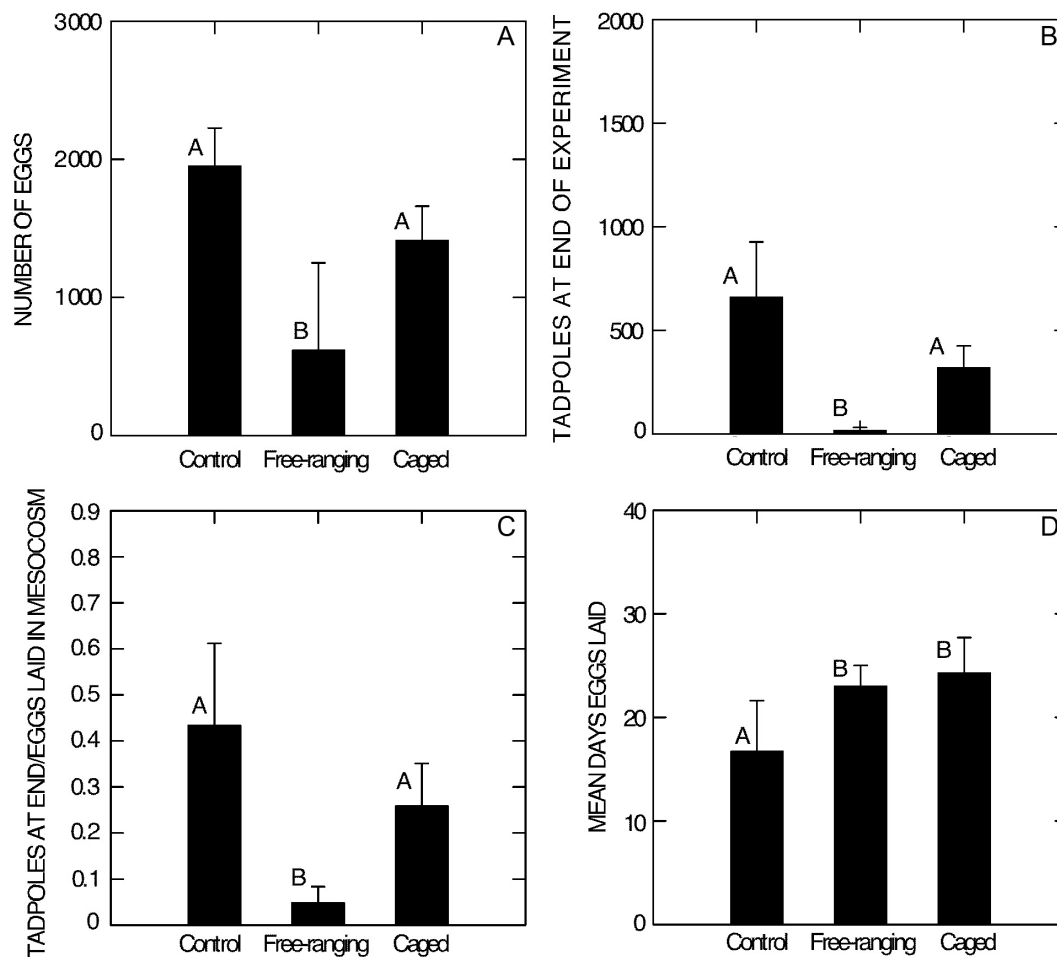


Fig. 1. Effect of western mosquitofish predator treatment on (A) mean number of gray treefrog (*Hyla versicolor*) eggs laid, (B) mean number of gray treefrog tadpoles at the end of the experiment, (C) mean proportional yield of tadpoles, and (D) mean day of experiment on which eggs were laid. Means are given ± 1 standard error. Means sharing the same letter are not significantly different.

to one-half those in other treatments) in mesocosms with free-ranging western mosquitofish. On its own, our observation of lower numbers of eggs laid in free-ranging predator mesocosms indicates that the presence of free-ranging western mosquitofish deters gray treefrog females from laying their eggs in ponds. It is not very surprising that gray treefrogs avoid ovipositing in mesocosms with free-ranging western mosquitofish given previous experiments showing that gray treefrogs (*H. versicolor* or *H. chrysoscelis*) avoid ovipositing in ponds with fish predators (Resetarits and Wilbur 1989, Binckley and Resetarits 2008, Vonesh et al. 2009), including *Gambusia* (Binckley and Resetarits 2003, Fryxell et al.

2015). Our results also suggest that females are able to differentiate the caged and free-ranging predator treatments, perhaps due to differences in the concentration of chemical cues (possibly perceived to be higher in the lethal mesocosms due to the fish being able to swim throughout the entire mesocosm), the composition of chemical cues (the consumption of tadpoles may produce additional chemical cues indicating increased risk [Fraker et al. 2009, Maag et al. 2012, Gazzola et al. 2018] which could deter oviposition), or potential physical contact between the mosquitofish and the ovipositing females (females are harassed to leave by nips or other contact by the free-ranging mosquitofish). An

additional potential contributing factor to the observed pattern of oviposition is that colonizing macroinvertebrates, especially potential tadpole predators, might affect oviposition choice. However, the abundances of potential predatory macroinvertebrates (e.g., odonates, dytiscid beetles) in our experiment were higher in both the control and the caged predator treatments than in the free-ranging predator treatments (J. J. Harmon and G. R. Smith, *unpublished data*). In addition, Resetarits and Wilbur (1989) found no effect of an odonate predator (*Tramea carolina* larvae) on the number of eggs laid by *H. chrysoscelis*. These two results suggest that the observed oviposition pattern is unlikely to be explained by avoidance of cues from macroinvertebrate predators.

What becomes clear when examining our results more closely is that the caged predator treatment also appears to have affected gray treefrog oviposition relative to the control mesocosms. While the mean total number of eggs deposited in these two treatments did not differ significantly (although the number of eggs laid in the non-lethal mesocosms was lower than in the control mesocosms), there was a significant delay (7–8 d) in the mean day on which eggs were laid in the non-lethal mesocosms relative to the control mesocosms. Earlier oviposition can be beneficial for the performance of tadpoles, including *H. chrysoscelis*, due to increased resources or decreased competition (Wilbur and Alford 1985), and thus, the difference in oviposition timing in our different predator treatments might have additional implications for the success of the gray treefrog tadpoles. Again, previous studies have shown that gray treefrog females will avoid ovipositing in ponds with caged fish predators (Binckley and Resetarits 2002, 2008, Vonesh et al. 2009, Kraus et al. 2011). However, what is novel about our study is that we allowed eggs and tadpoles to remain in the mesocosms throughout the entire experiment. The previous experiments cited above removed eggs daily. Our experiment therefore mirrors the situation in a natural pond more closely than these previous studies. The fact that the number of eggs laid did not differ between the control and caged predator treatments, but the mean day of oviposition did, strongly suggests that gray treefrog females show a shift in their

decision-making process over the course of the experiment. Specifically, we argue that early in the experiment when there were few eggs or tadpoles in any mesocosm, females were ovipositing in the control mesocosms to avoid the predator. Later in the experiment, females began to shift to ovipositing in the caged predator mesocosms to avoid the presence of competitors in the control mesocosms while also avoiding the higher predation risk in the free-ranging predator mesocosms. This shift in oviposition preference by the gray treefrogs in our experiment matches the prediction of the Blaustein (1999) model and an ideal free distribution (Fretwell and Lucas 1970), and indicates that the females are making threat-sensitive decisions with regard to where they lay their eggs. These results are consistent with previous experiments where eggs were removed shortly after oviposition. For example, *H. chrysoscelis* and *H. squirella* only oviposited in mesocosms with fish on nights when the most eggs were laid (Binckley and Resetarits 2003, 2008). These results contrast with Buxton et al. (2017) who found that when given a choice among ponds with *G. affinis*, conspecific eggs, or both *G. affinis* and conspecific eggs, *P. triseriata* did not differentiate among the three types of ponds and Resetarits et al. (2018) who found no effect of conspecific density on oviposition by *H. chrysoscelis* in the presence of fish.

Relative roles of pre- and post-colonization effects on gray treefrog tadpole production

Both pre- and post-colonization effects of western mosquitofish appear to be responsible for the drastic reduction of gray treefrog tadpoles in the presence of free-ranging western mosquitofish. First, there is a clear reduction in the number of eggs laid in the free-ranging predator mesocosms (see previous section). Thus, inhibition of oviposition (i.e., a pre-colonization effect) reduces the size of the initial pool of colonizers in the experimental ponds with free-ranging western mosquitofish. Second, there is also a significant reduction in the yield of tadpoles (i.e., survivorship from oviposition to the end of the experiment) from the eggs laid in a mesocosm in the free-ranging predator mesocosms compared to the control and caged predator mesocosms, suggesting that reduced tadpole production is also a consequence of the lethal presence of the western

mosquitofish. The yield in non-lethal predator mesocosms did not significantly differ from the yield in control mesocosms, suggesting that it is indeed predation by the free-ranging western mosquitofish that is driving these post-colonization effects rather than an indirect trait-mediated interaction. Based on evidence from a laboratory experiment that found western mosquitofish did not consume gray treefrog eggs, but rather consumed their hatchlings or tadpoles (Smith and Smith 2015, see also Grubb 1972), we argue that the reduced yield in these mesocosms is due to consumption of hatchlings or tadpoles rather than eggs. Western mosquitofish therefore have great potential to negatively impact the distribution and successful recruitment of gray treefrogs through both pre-colonization and post-colonization effects. Indeed, other studies of constructed wetlands and experimental mesocosms have found the abundance of hylid tadpoles reduced or eliminated by the presence of free-ranging *Gambusia* (Preston et al. 2012, 2017, Shulse et al. 2013, Fryxell et al. 2015).

CONCLUSIONS AND BROADER IMPLICATIONS

In conclusion, our experiment demonstrates that *H. versicolor* differentially oviposit in experimental ponds in a manner consistent with the relative risk associated with the ponds. Our results also demonstrate that this ability to assess risk is quite refined, allowing differentiation between ponds with no, caged, and free-ranging predators. In addition, there was a shift in oviposition choice over time such that shifts in the relative risk structure among pond types and oviposition choice were aligned (i.e., shift from primarily ovipositing in control ponds to including caged predator ponds as the season progressed as the risk from competition from conspecifics increased in control ponds). Finally, our experiment demonstrates that western mosquitofish, an invasive predator, can drive the distribution and abundance of gray treefrogs, and likely other amphibians, through both pre-colonization and post-colonization mechanisms.

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